THE

AMERICAN NATURALIST

VOL. XXV. FEBRUARY, 1891. 291.

RECENT STUDIES OF THE VERTEBRATE HEAD.

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THE view that the vertebrate head is composed of several segments, comparable to those of the trunk, has of late years formed the basis of almost innumerable essays; but the problems connected therewith cannot yet be regarded as solved. It is, indeed, universally admitted that the head is composed of segments or metameres; but the number of segments and the limit of each segment are points upon which there is far from unanimity of opinion. A study of the skull, as was first pointed out by Goethe, leads to one conclusion, while a study of the muscle-plates or myotomes of the embryo gives greatly different results. Then the brain itself in its early stages shows marked evidence of metamerism, while the nerves arising from the brain can be more or less clearly divided into segmental groups which can be compared to the undoubtedly segmental spinal nerves.

In the following pages I have presented, in a very condensed form, the results of some recent studies in this direction. In these abstracts the nerves are referred to by Roman numerals, in accordance with the commonly received ideas of their sequence: I., olfactory; II., optic; III., oculomotor; IV., trochlearis; V., trigeminus; VI., abducens; VII., facial; VIII., auditory; IX., glossopharyngeal; X., vagus; XI., spinal accessory; XII., hypoglossal.

In the lizard, according to Hoffmann ('88–'89), the myotomes of the head agree very closely with the same in the chick

and Selachians. But the fourth seems to be wanting, and corresponding in position to the third myotome are two small cellular masses, not connected with each other, out of which are developed the muscles externus rectus and retractor bulbi. Between the vagus nerve and the first cervical spinal nerve are four myotomes, the cephalic of which is rudimentary. The oculomotor, trochlear, and abducens nerves are not described in their earliest stages. The III. with a broad origin springs from the base of the midbrain, and innervates the muscles derived from the first head-cavity. The IV. arises as a large cellular outgrowth from the place where the roof of the midbrain passes into the hindbrain, and resembles in every respect the "Anlagen" of the dorsal cranial nerves, sending an extension to the epidermis. The absence of a trochlear ganglion in the serpent, bird, and Selachians, and its presence in the lizard, gives rise to the query whether the trochlear nerve may not primarily have been the motor nerve of the protective organs of the parietal eye. The VI. springs by 10–12 fine fibres from the base of the medulla oblongata, and innervates the muscles derived from the two cellular masses that appear to belong to the third head-cavity. The V., VII.–VIII., IX., and X. nerves take their origin from the neural ridge, in a manner similar to the dorsal roots of spinal nerves, and their respective ganglia unite with the epidermis above the branchial arches. Between the V. and VII.–VIII. the neural ridge early aborts. The ophthalmic ganglion of the V., from its development on a dorsal root and its anastomosing with the III. nerve, a ventral root, is regarded as homologous to a dorsal ganglion. The ganglion of the VII.–VIII. nerve divides into two portions, the anterior part being the proper ganglion of the facial nerve, the other forming the auditory ganglion. The accessorio-vagus nerve arises by a broad base extending from the IX. nerve to the second cervical spinal nerve. Later the neural ridge loses its connection with the brain, and becomes a commissure between the second cervical nerve and the caudal vagus root, so the X. nerve then arises by 5–6 roots. The hypoglossus originates by four roots, the caudal root being a branch of the first cervical spinal nerve. Anterior to the roots of the hypoglossus are two rudi-

mentary somites, to the caudal of which apparently belongs a nerve of transitory duration. Froriep had already discovered four somites in the occipital region of the chick, but it will be seen that in the lizard there are five somites in this region. The two cephalic roots of the hypoglossus possess neither ganglia nor dorsal roots; the condition of the third root in this respect has not been determined; the first cervical nerve has a transient ganglion, and the second cervical a permanent ganglion. The hypoglossus thus seems to represent a complex of true spinal nerves, whose ganglia and dorsal roots have partially or completely degenerated. According to Hoffmann ('89), on the hinder portion of the lizard's brain appears an evident segmentation. Other authors had previously noticed this. Hoffmann finds in the hindbrain and medulla seven segments. From the caudal of these springs the X. nerve; from the next, or sixth, the IX.; opposite the fifth is the ear vescicle; from the fourth arises the VII.–VIII.; from the third none; from the second the V.; from the cephalic border of the first segment the trochlear nerve primarily takes its origin, though later shifting over to the midbrain.

Rabl ('89) considers the vertebrate head as consisting of two regions: a cephalic or proximal unsegmented, and a caudal or distal segmented region.[1] The ear vescicle forms the boundary between the two portions, but is to be reckoned with the proximal. The mesoderm of the proximal section may be divided into segments which neither in mode of origin nor in further development can be compared with protovertebræ. The five distal somites arise exactly as the protovertebræ. The first protovertebra to appear is the fifth head somite of Van Wijhe, or the first distal somite. The musculature and connective tissue of the distal somites develop in the same portions as in the protovertebræ of the body. Dorsal and ventral nerve roots occur in this region as in the body. In their origin the proximal somites show scarcely even a distant relationship with the structure of protovertebræ. The proximal somites cannot be called primary, for they appear later than the protovertebræ. The muscles of the proximal re-

[1] Kastschenko had observed in Pristiurus and Scyllium that at no period did the mesoderm of the anterior portion of the head appear segmented.

gion arise almost entirely in portions where in the protovertebræ connective tissue originates, and vice versa. There is no differentiation of myotomes and sclerotomes in the proximal somites. There are two primary nerves in the cephalic portion, the V. and VII.–VIII., but these do not arise from a continuous neural ridge. The cephalic border of the neural ridge forms a delicate strand uniting with the triangular part of the trigeminus Anlage, which becomes the ciliary ganglion. In later stages, answering to the direction of this delicate strand, extend the oculomotor and trochlear nerves. The oculomotor and trochlear nerves are thus to be considered as secondarily derived from the trigeminus, and the eye-muscles perhaps from the musculature of the first branchial arch innervated by the V. From researches on Selachians, birds, and mammals it is concluded that the III. and IV. nerves arise on the dorsal border of the midbrain. The primary nerves of the caudal region of the head are the IX., X., and hypoglossus, the latter consisting of the ventral roots of the region. The IX. and X. arise from a continuous neural ridge in a series with the dorsal roots of the true spinal nerves. The opinion of Beard, that the "Anlagen" of the dorsal cranial and spinal roots develop prior to and independent of the neural tube, is erroneous. The homology of the spinal ganglia to the parapodial ganglia of Annelids cannot be established till it is proved that the spinal ganglia grow out of the ectoderm independent of the neural tube. Rabl bases his observations on embryos of *Torpedo ocellata.* The unsegmented mesoderm of the head in the Craniota he compares with the unsegmented forward extension of the first primitive segment in Amphioxus. In the head region of Amphioxus are two stout nerves, which cannot be compared with spinal nerves. Rabl thinks they may be homologous with the V. and VII.–VII. of the Craniota.

In reply to Rabl, Dohrn ('90*a*) notes that the former repeats the mistake of Balfour in deriving the dorsal roots of the spinal nerves from the neural ridge. In all Selachians the dorsal roots of the spinal nerves grow out of the ganglia into the neural tube. The sensory fibres of the cranial nerves (V., VII.–VII., IX., and X.) grow out from the ganglia into the brain, while the motor fibres spring from the cells of the lateral columns and enter the ganglia.

The neural ridge arises as a cell-growth from the closing portion of the neural tube, as Rabl says. Neither His's "Zwischenstrang" nor Beard's ectodermal ganglion-anlage theory is tenable. The cells of the neural ridge, that do not form ganglia, atrophy. The neural ridge may thus be regarded as merely the forerunner of the ganglia. The gaps between the Anlagen of the V., VII.–VIII., and IX. nerves do not prove the absence of a continuous neural ridge in that region, but rather are points of atrophy. Rabl is correct in saying that a nerve-strand arises at the cephalic border of the neural ridge. The cell-mass from which this springs is anterior to the ciliary and gasserian ganglion Anlagen. In Torpedo a true ganglion is found derived from this cell-mass, but it later loses connection with the neural tube and neural ridge. After isolation nerve-fibres grow out from this ganglion, thus proving that sensory nerve-fibres and sensory root-fibres arise not from the neural tube, but from the cranial and spinal ganglia. The fibres of this isolated ganglion enter into such close relation with the trochlear nerve as to appear to belong to it. This ganglion and its outgrowth of fibres appear to represent the nerve ophthalmicus superficialis minor. The III. nerve arises by 3–7 roots from the base of the midbrain, and no medullary cells pass out with it. The ganglion, which seems to belong to this nerve, is really derived from the ciliary ganglion. The III. and IV. do not have their origin in the cephalic portion of the neural ridge. The VI., as well as the III., spring from the anterior column of the medulla oblongata. It arises by 4–6 roots. The hypoglossus is in no way connected with the vagus. It is to be regarded as formed from the ventral roots of one or more spinal nerves, as Balfour thought. Van Wijhe found extending over the eighth and ninth myotomes an outgrowth of the neural ridge, interpreted by him as representing rudimentary ganglia of the second and third hypoglossal roots. Froriep first established the existence of rudimentary ganglia of the hypoglossus. Ostroumoff finds in Pristiurus two spinal ganglia answering to the last two roots of the hypoglossus. Dohrn states that the hypoglossus has as many ganglio Anlagen as there are ventral roots, the first being merely a thickening of the neural ridge. It is impossible to

classify the V. and VII.–VIII. nerves in contrast to the IX. and X. All four are connected with the organs of the lateral line, while the spinal nerves take no part in the latter structures. The motor roots of all four spring from the lateral column, and pass into the ganglia, while no motor fibres go into the spinal ganglia. In Selachians, at the time the sensory roots of the glossopharyngeus and vagus enter the medulla oblongata, there appears in this region a folding or furrowing of the walls of the neural tube, similar to that seen in the spinal cord. In this segmentation the roots of the IX. and X. nerves correspond in position to the furrows separating the metameres, just as the furrows in the metamerism of the spinal cord answer to the sensory nerve-roots. The probability that the vagus is a polymere whose components were originally similar to spinal nerves, the similarity of the V. and VII.–VIII. nerves to the IX. and X. in development and functional differentiation, and the fact that the neural ridge can be traced anteriorly into the VII.–VIII. anlage, render Rabl's hypothesis of unsegmented cranial mesoderm untenable.

Dohrn's recent contributions ('90*b*) to our knowledge of primitive cranial segmentation must be regarded as epoch-making. In embryos of *Torpedo marmorata*, stage F of Balfour, 12–15 myotomes are found anterior to the glossopharyngeal region. Rabl refused to refer any segmentation to this region. Van Wijhe found four somites. These 12–15 myotomes pass ventrally into the lateral plates, which form the cranial cœlom, and out of which come the "head-cavities." In stage G the myotomes are considerably coalesced, and the more the development goes on the more the obliteration of myotome boundaries. Van Wijhe's mandibular somite is made up of 3 myotomes, the hyoid of 3, and the fourth somite of 2–3. The segmentation recognized by Van Wijhe is thus apparently secondary. The myotomes of the head are throughout comparable to the myotomes of the body. The cranial motor nerves show a metamerism. The III. nerve arises by 4–7 separate fibres, and innervates the muscles of the premandibular head-cavity, which is a multiple of myotomes. The VI. originates also as a multiplex of fibres, and innervates the

muscles of the third head-cavity, which is also composed of several myotomes. Both nerves spring from the anterior columns, and are homodynamous with motor spinal nerves. The IV. nerve emerges on the dorsal border of the brain, but whether it is homodynamous with the cranial ganglionic motor fibres, or with the motor spinal nerves, is uncertain. The ganglionic motor fibres, viz., those of the V., VII.–VIII., IX., and X., arise from the lateral columns. These fibres greatly converge in passing to the ganglion-anlagen of the respective nerves, and it may be assumed that at one time the fibres arose as separate nerves, each belonging to its myotome. Marshall believes the olfactory nerve to be an outgrowth from the anterior portion of the neural ridge. Beard advances the same view. His found that in human embryos the olfactory ganglionic cells and nerve-fibres originated from the epithelium of the nasal vescicle. Dohrn confirms the same in Selachians. Rudimentary ganglia are found in the anterior part of the V. Anlage, in the anterior part of the VII. Anlage, and in the anterior part of the IX. and X. We see indications of a centralizing process which has resulted in the reduction in number of the primitive ganglia. Displacement and suppression has taken place in the visceral mesoderm of the head. The premandibular, mandibular, and hyoid head-cavities are to be considered as multiples of original head-cavities, in which serial origin the lateral plates share. The fact that the embryonic vascular system is similar throughout would indicate that it originated at a time when the body was not yet differentiated into metameres. The difference in direction of the blood-currents in the aorta and the carotids can be explained by the hypothesis that the current in the latter has been reversed by the suppression of preoral arterial arches. By this hypothesis it may be assumed that at one time there was no separation between aorta and carotids. In consequence, the existing mouth is derived from the coalescence of one or more pairs of gill-clefts, and there must have been a time when the present mouth did not exist. Thyroid and hypophysis must have had a bilateral structure; so that a median passage could be left for the conus arteriosus. The aorta shares in two segmentations: one that of the

branchial arches, the other that of the vertebral arteries; the one of the branchiomeres, the other of the myotomes. The existing branchiomeres do not appear to be secondary to the myotomes, but secondary to primary hypothetical branchiomeres. In the hyoid and mandibular arches, and in the region of the head-cavity supplied with the III. nerve, are to be assumed a greater number of primitive branchial clefts. Hyoid and spiracular clefts are to be considered as multiples of branchial clefts. The irregularity seen in the posterior branchial arches is connected with the changes that have caused the coalescing of branchial arches. Thyroid, mouth, hypophysis, and nose are evidently related to the branchial system. Gegenbaur holds that the branchial skeleton is secondarily derived from ribs. But the ribs are dorso-lateral structures, and the branchial arches ventral. If the latter are secondary articulations of the vertebral column, then traces of the apophyses should be found. But as this does not occur, the branchial skeleton is to be regarded as of independent origin. The hyoid and mandibular cartilages then represent multiples, and cartilaginous girdles, which have functioned as branchial arches, now enter into the composition of the skull.

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(*To be continued.*)